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Establishing surveillance areas for tackling the invasion of *Vespa velutina* in outbreaks and over the border of its expanding range

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Abstract

The yellow-legged hornet *Vespa velutina* is an invasive alien species in many areas of the world. In Europe, it is considered a species of Union concern and national authorities have to establish surveillance plans, early warning and rapid response systems or control plans. These strategies customarily require the assessment of the areas that could be colonised beyond outbreaks or expanding ranges, so as to establish efficient containment protocols. The hornet is spreading through a mix of natural diffusion and human-mediated transportation. Despite the latter dispersion mode is hardly predictable, natural diffusion could be modelled from nest data of consecutive years. The aim of this work is to develop a procedure to predict the spread of the yellow-legged hornet in the short term in order to increase the efficiency of control plans to restrain the diffusion of this species. We used data on the mean distances of colonial nests between years to evaluate the probability of yellow-legged hornet dispersal around the areas where the species is present. The distribution of nests in Italy was mainly explained by elevation (95% of nests located within 521 m a.s.l.) and distance from source sites (previous years' colonies; 95% within 1.4–6.2 km). The diffusion models developed with these two variables forecast, with good accuracy, the spread of the species in the short term: 98–100% of nests were found within the predicted area of expansion. A similar approach can be applied in areas invaded by the yellow-legged hornet, in particular beyond new outbreaks and over the border of its expanding range, to implement strategies for its containment. The spatial application of the models allows the establishment of buffer areas where monitoring and control efforts can be allocated on the basis of the likelihood of the species spreading at progressively greater distances.

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Keywords
Asian yellow-legged hornet, invasive species, control plans, monitoring, nest distance, predictive models

Introduction

Implementing cost-effective management plans for invasive alien species requires the development of tools that can improve the performance of control activities. A control plan should foresee different stages, including assessment of feasibility, implementation, monitoring and evaluation of the results (Braysher 1993, Bertolino et al. 2005). Monitoring is a necessary step to both verify whether control activities are effective and to provide feedbacks to improve management strategies (Braysher 1993, Bertolino and Viterbi 2010). Prioritisation to support a cost-effective allocation of resources is part of decision-making in species management (McGeoch et al. 2016). When the goal of the management plan is the containment of a species, it is necessary to evaluate where the species is most likely to spread in the short term, in order to better localise control activities. This requires assessing which areas should be surveyed and the intensity of the monitoring activity that should be allocated in each area (Hauser and McCarthy 2009).

Modelling procedures are customarily used to predict the spatial dynamics of invasive species dispersal over time. Models are built by fitting empirical data into mathematical functions or using field data to simulate population dynamics to be spatially projected (Sharov and Liebhold 1998, Gilbert et al. 2004, Shatz et al. 2016). While these procedures represent a powerful tool to provide information to improve management strategies, they require good knowledge about the ecology and dispersal abilities of the target species and are mainly used for simulations at large scales (Hastings et al. 2005).

The yellow-legged hornet (*Vespa velutina* Lepeletier, 1836) is a social wasp, native to tropical and subtropical areas of Indo-China (Archer 1994, 2012). The species established itself in non-native countries such as France (Haxaire et al. 2006), South Korea (Choi et al. 2012) and Japan (Ueno 2014). From France, the species spread to neighbouring countries (Grosso-Silva and Maia 2012, Rome et al. 2013, Bertolino et al. 2016). In Italy, the yellow-legged hornet was detected for the first time in Liguria in 2012 (Demichelis et al. 2014); afterwards the hornet started to spread in this region mainly along the coastline (Porporato et al. 2014, Bertolino et al. 2016) and, in 2017, the species had colonised an area of at least 1,110 km^2 (Lioy et al. 2018). In Europe, the species is considered invasive, both for its expansion capabilities at European scale (Fournier et al. 2017, Robinet et al. 2017, Barbet-Massin et al. 2018) and the impacts that it could produce by preying on honey bees and native insects (Beggs et al. 2011, Monceau et al. 2013, 2014). Although the presence of the species is not considered a problem for human-health (De Haro et al. 2010), by frequently establishing colonial nests in urban areas, the yellow-legged hornet could generate social impacts due to citizens' perception of fear of possible stings, which could lead to thousands of phone calls from people asking for destruction of the nests (Liu et al. 2015, Tabar et al. 2015, Sumner et al. 2018). Moreover, the management of phone calls and the maintenance of control activities lead to significant economic costs (Robinet et al. 2017). For these

reasons, attempts to control this species have been undertaken in many countries since its early stage of invasion (Monceau et al. 2014, Bertolino et al. 2016, Rodríguez-Flores et al. 2018). Its recent inclusion in the European list of invasive alien species of Union concern (Reg. EU 1141/2016) requires Member states to implement surveillance protocols and control strategies.

The colony of the yellow-legged hornet is initiated by a single inseminated queen that builds a primary nest after overwintering, thus producing the first workers. Afterwards, during the warm season, they enlarge the primary nest or build a secondary nest; with time, nests grow up to a sphere of about 50–100 cm in diameter, containing several thousands of hornets. From September onwards, reproductive animals emerge and mate; in late autumn or winter, all nests die, while newly-mated queens search for a place where they can overwinter and, the following year, they start a new cycle (Archer 2012, Monceau et al. 2014, Rome et al. 2015). As for many other arthropods, invasions may proceed in smooth advances of the main front or in jumps. In the first case, species spread by natural dispersal of animals, giving rise to a diffusion-like process (Suarez et al. 2001). Conversely, jumps usually occur when the dispersal is human-mediated (Hastings et al. 2005, Homans and Horie 2011). In the case of the yellow-legged hornet, this happens usually by the accidental movement of goods (e.g. straw, soil, timber) that contain dormant overwintering queens or by active adults travelling as hitchhikers on vehicles, though long-distance active dispersal could not be excluded in many cases (Marris et al. 2011, Bertolino et al. 2016, Robinet et al. 2017). Human-mediated transportation is hardly predictable and therefore only a large scale monitoring system could allow the rapid finding of new sites of invasions. On the contrary, the natural dispersal could be forecast with observational data of presence recorded year by year. Distances covered by yellow-legged hornets to establish new colonies are not known. Although queens are considered efficient flyers, published studies that demonstrate in the field the flying abilities of new founder queens to disperse from their original colony and create their own colonies are, however, still lacking. Population spread rate has been estimated in some countries and values are non-consistent, suggesting that spread rate could be different case-by-case, for example, depending on environmental and morphological characteristics of the invaded area. Robinet et al. (2017) estimated a mean spread rate of the population of 78 km/year (range between 75–112 km/year) in France, Bertolino et al. (2016) a mean spread rate of 18 km/year in Italy and Choi et al. (2012) a diffusion of 10–20 km/year in South Korea. Sauvard et al. (2018) tested the flying abilities of workers in laboratory conditions throughout flight mill experiments; they demonstrated that workers are able to fly on average from 10 km to 30 km per flight test. This does not means that workers in the field actually keep these flying values, since, in natural conditions, they are not forced to fly up to their maximum limit. It is likely that queens are also efficient flyers, but is not probable that queens in dispersion will travel to their maximum flight limit, but will probably stop to build their new colonies where they find a suitable spot (cost-benefit behaviour).

Habitat suitability and the possible spread of the yellow-legged hornet in Europe have already been modelled at large scales with different approaches (Ibáñez-Justicia and

Loomans 2011, Villemant et al. 2011, Fournier et al. 2017, Robinet et al. 2017, Keeling et al. 2017). Some of these models have recently been validated and the prediction has proved to be adequate for real occurrence data (Barbet-Massin et al. 2018). However, if large scale modelling (i.e. European level) allows understanding long-term potential distribution of the species, their use in control activities is limited, since control plans are developed locally based on nest dynamics and distribution. A detailed description of yellow-legged hornet nest dynamics has been reported and modelled for a municipality in France (Franklin et al. 2017, Monceau and Thiery 2017); however, the scenario of Andernos, in which the species has established a viable population and reached high-density values, could be different from new invaded areas of other European countries.

Though the fast spread of the yellow-legged hornet in Europe clearly shows that control activities have been generally ineffective, modelling scenarios indicate that increasing the percentage of removed nests could slow down the spread rate (Robinet et al. 2017). Currently, control plans for the yellow-legged hornet are based on finding and destroying the maximum number of nests, ideally all, present in the managed area before the dispersal of the new queens later in the year. Therefore, an efficient monitoring system must be established to locate colonial nests. This should consider not only the present known range of the species, but also an external buffer zone where it is likely that founder queens could disperse and establish new colonies in the short term. Customarily, the monitoring effort is high at the front of a species expansion and decreases with the distance. How fast it decreases is often connected with the species spread rate and human-resource availability. In the case of *V. velutina*, however, an optimal allocation of the effort could be established with information on the likelihood of nests being built at progressive distances from the frontline. With this information, the monitoring effort in an area could be calibrated with the likelihood of dispersal, increasing the cost-efficiency of the monitoring scheme.

The aim of this study is to create an adaptive predictive model of expansion for the yellow-legged hornet, which could be applied in any new invaded areas to both predict the hornet natural expansion and to allocate the available monitoring and control resources, based on species colonisation probabilities. We used data on the mean distances of colonial nests between years to infer the likelihood that queens will naturally spread the year after at a certain distance from the invasion front. This approach allows modelling species spread with no need for taking account of local characteristics (e.g. environmental characteristics, climatic conditions, carrying capacity) in the perspective of establishing early warning and rapid response systems for this species in new invaded areas.

Methods

The western part of Liguria, where many nests are discovered every year, is the main Italian district colonised by the yellow-legged hornet (Bertolino et al. 2016). The species has been detected in this area since 2012: *i*) a male was trapped in Loano at about 70 km from the French border (Demichelis et al. 2014), but no nests were detected in

the following 5 years in this area; *ii*) one hornet was trapped in Ventimiglia at about 2 km from the French border. First nests were discovered in 2013 (Porporato et al. 2014) in some municipalities near France (5 nests in the cities of Dolceacqua, Vallecrosia and Bordighera). The species has also been observed in eastern Liguria, Piedmont, Lombardy, Veneto and Tuscany, but here, observations were scanty and only few nest were reported (Lioy et al. 2018). Therefore, the main colonised area of Liguria has been selected as the study area for the development of the predictive model.

The analysis is based on verified nest positions collected during four years (2014–2017), considering both nests discovered in spring during the foundation phase, which represents a small proportion of the data (2–3% of the total nests discovered in each year) and developed nests discovered later in the season (data available as Suppl. material 6; 2013 nests were not included due to the small dimension of the sample size). Since nests are difficult to detect, in particular before the fall of the leaves, a great effort was dedicated in creating an enlarged monitoring network, including multiple sources of information. Nests were reported by: *i*) citizens and beekeepers; *ii*) firefighters, civil defence teams and local authorities that received reports from citizens; *iii*) a network of more than 1,000 beekeepers with 1,638 monitoring stations established in a wider area of Liguria and Piedmont (Suppl. material 5). Nests were also actively searched for by monitoring teams of the LIFE STOPVESPA project involved in field survey. These teams were *i*) verifying the reported nests, *ii*) verifying the presence of hornets in apiaries and searching for nearby nests and *iii*) actively monitoring the environment, searching for nests also with the use of binoculars. The teams were also active during autumn and the beginning of winter; this allowed the detection of additional nests that might have been hidden by tree leaves in the previous months. The teams' activity was fundamental to discover nests further away from urban areas and not frequented by people. Dissemination activities with hunters and fishermen allowed the involvement of people who frequented different environments, increasing the possibilities to detect nests in natural areas or riverbeds. Data were aggregated by year and analysed with R and QGIS (QGIS Development Team 2015, R Core Team 2015).

For each year, the area, colonised by the yellow-legged hornet, has been estimated by a range analysis, with the kernel method of the R's package ADEHABITATHR (Calenge 2006). The limits of the estimated ranges of each year were used as a starting point to evaluate the areas at different likelihood of colonisation in the subsequent year. Outlier nests, located in Liguria distant from the main colonised area, were treated as potential further source of diffusion in addition to the border of the expanding range.

In a natural diffusion process, queens which found new colonial nests in one year originated from nests of the year before (source sites). The set of these measures can be used as a forecast of distances where the nests could be found the following year. Accordingly, a nearest-neighbour analysis was used to estimate the distances between nests of each year from source sites of the previous years. We then used these measures to develop a probability model of the distances where queens could establish their nests in the following year. From the estimated distances, a probability plot was constructed respectively for years 2015, 2016 and 2017. A non-linear regression analysis was used

to estimate the equations with the best fitting for the data. These equations were used in QGIS to build the model: *i*) a grid with 100 m × 100 m cells was overlapped to the area outside the yellow-legged hornet's range of a single year; *ii*) the distances between the centroids of each cell and the nearest source sites was calculated and the species probability of colonisation for each cell of the grid was estimated according to the previous equation on nests distances from sources. This process was repeated for each year, to create predictive models for years 2016, 2017 and 2018.

Yellow-legged hornet's nests in Italy are not distributed with uniformity along the elevation (Fig. 1). Therefore, the ranges estimated applying the predictive models were clipped at three different altitudes (700, 900 and 1,200 m a.s.l.), thereby producing three different scenarios for each year. The criteria that guided the selection of these limits are: 99% of the nests were found within 700 m a.s.l.; only one nest was discovered at 906 m a.s.l. in Piedmont (Porporato et al. 2014); adult hornets have been reported up to 1,200 m a.s.l.

The predictive models for years 2016 and 2017 were validated comparing the probabilities of colonisation associated with the position of nests (i.e. position of the nest found in that year) for their respective years against the probabilities associated to pseudo-presence data, which are points randomly positioned in the areas of colonisation predicted by the models. A ROC analysis (Fielding and Bell 1997) that allowed the calculation of the area under the ROC function (AUC) was used for the validation procedure (Sing et al. 2005).

To further evaluate the importance of elevation and distance of nests from source sites when modelling the yellow-legged hornet expansion, a generalized linear model (GLM) with binomial distribution and logit link function was used to compare the variables associated with 1,130 points of presence (nests' positions) and 1,130 random points of pseudo-absence. Five variables (one species-dependent and four environmental) were selected as explanatory variables of the GLM: *i*) distance of nests from source sites (nests of the previous year), which is the species-dependent variable that has been hypothesised as the main explanatory variable; *ii*) elevation upon the sea level; *iii*) surface aspect, grouped in the eight corresponding factors of 45° each (north, north-east, east and so on); *iv*) distance between nests and water resources; *v*) land cover (Regione Liguria 2015, 1:10.000). Nine macro-categories were identified for the land cover variable, on the basis of main environmental characteristics of the study area: urbanised, agricultural, woodlands, riparian areas, coastal areas, alpine grasslands, vineyards and olive groves, greenhouses, other environments. GLM results were compared with AIC in order to select the best model. Climate conditions were not considered because they do not change considerably in short distances, while data on carrying capacity, according to habitat suitability, are not available.

Results

The nearest-neighbour analysis highlighted that nests of the yellow-legged hornets were mostly located within short distances from source sites: 50% of nests were found within 203–668 m from nests of the previous years and 95% within 1.4–6.2 km

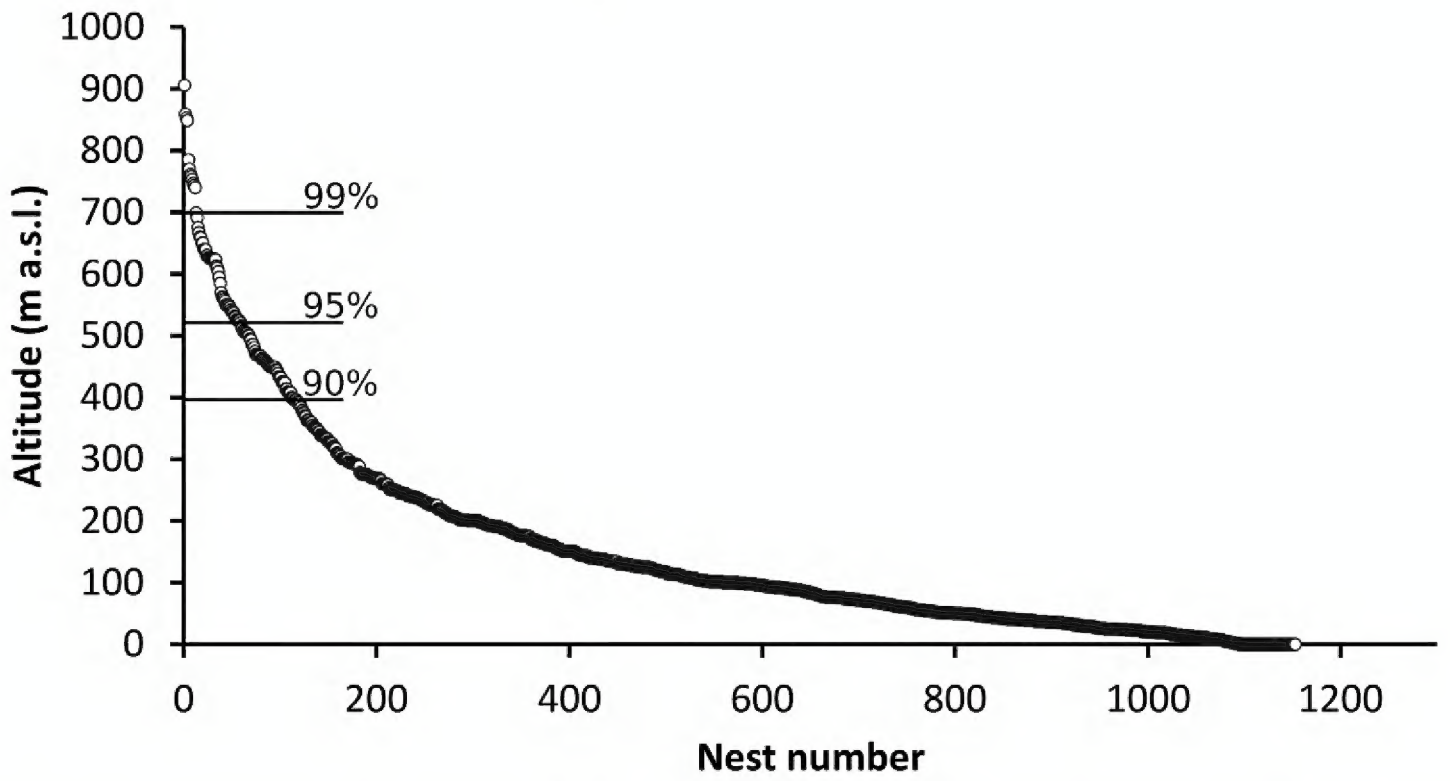

Figure 1. Distribution of yellow-legged hornet nests along the altitude gradient: most of the nests are at low altitude, 90% of them within 396 m, 95% within 521 m and 99% within 699 m a.s.l. Nests were discovered up to 906 m a.s.l.

Table 1. Maximum distance of nests from source sites (nests of the previous years) grouped in proportion intervals for years 2015, 2016 and 2017.

Proportion of nests (%)	Distance from source sites (m)		
	2015	**2016**	**2017**
50	668	411	203
75	1,852	864	450
90	3,222	1,637	924
95	6,211	2,633	1,372
100	10,912	11,162	3,513

(Table 1). Few nests were found at greater distances from source sites, up to about 11 km in 2015–2016, but only at 3.5 km in 2017.

The probability of finding yellow-legged hornet nests over the limits of its colonisation range consequently decreases rapidly with increasing distances from source sites (Fig. 2). The trends were explained by logarithmic functions (2015: $R^2 = 0.97$; $F_{1,230} = 7504$; $p < 0.001$; 2016: $R^2 = 0.94$; $F_{1,484} = 7738$; $p < 0.001$; 2017: $R^2 = 0.92$; $F_{1,411} = 4330$; $p < 0.001$).

The spatial application of the probabilistic models, developed to predict the expansion of the yellow-legged hornet in 2016, is reported in Fig. 3 for the three altitudinal ranges. Similar maps for 2017 and 2018 are reported in Suppl. materials 1 and 2, respectively. For each model, the amount of area at different level of probability of colonisation has been estimated in probabilities' intervals (Table 2 for 2016 and Suppl. materials 3 and 4 for 2017 and 2018).

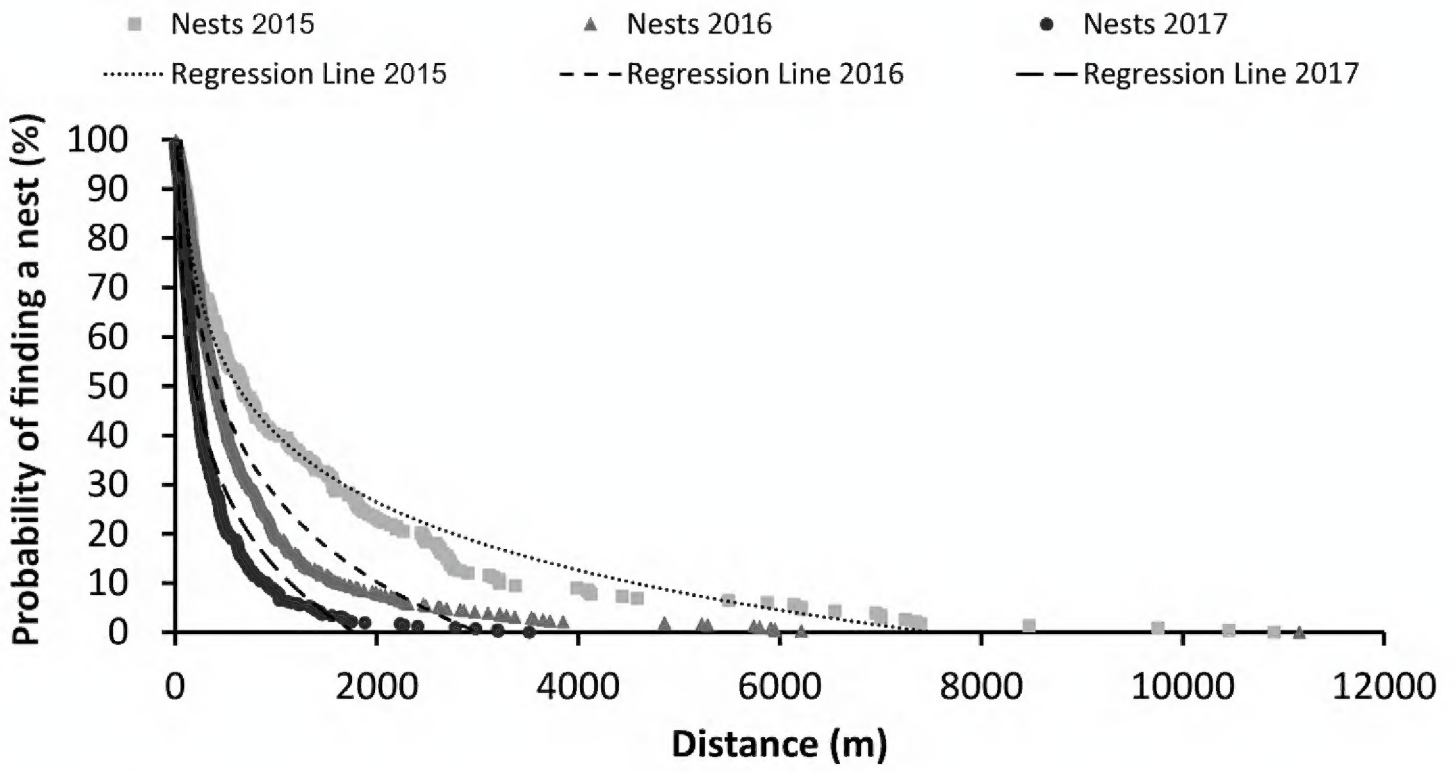

Figure 2. Nests distances from source of diffusion of the previous years: the distance of nests from a possible source of diffusion is given on the x-axis, while the probabilities to find a nest on the y-axis. The lines represent the logarithmic regression models of the data (regression line 2015: $y = -0.2\ ln\ (x) + 1.785$; $R^2 = 0.97$; regression line 2016: $y = -0.25\ ln\ (x) + 2.0057$; $R^2 = 0.94$; regression line 2017: $y = -0.227\ ln\ (x) + 1.6967$; $R^2 = 0.92$).

Table 2. Predictive models of year 2016: areas to be monitored for each probabilities range of colonisation by the yellow-legged hornet. The areas of the three elevation scenarios are reported: A) 700 m a.s.l; B) 900 m a.s.l; C) 1,200 m a.s.l.

Probabilities range (%)	Area A (km²)	Area B (km²)	Area C (km²)
90–100	0.04	0.04	0.08
80–90	0.07	0.10	0.16
70–80	0.21	0.23	0.33
60–70	0.30	0.38	0.68
50–60	1.15	1.32	2.16
40–50	3.50	4.04	5.91
30–40	13.97	15.03	19.77
20–30	59.67	68.02	81.47
10–20	220.48	258.38	296.23
0–10	232.61	263.37	283.05
Total	**532.00**	**610.91**	**689.84**

The predictive models for years 2016 and 2017 have been tested with the position of nests actually discovered in those years. Of the nests located in 2016 outside the range of the previous year, 98% were included in the predicted areas of expansion of the two scenarios at 900 m and 1,200 m a.s.l. and all the nests in 2017 were included in the predicted areas of the three scenarios. The analysis of the area under the ROC function highlights a difference between probabilities associated with nests' position

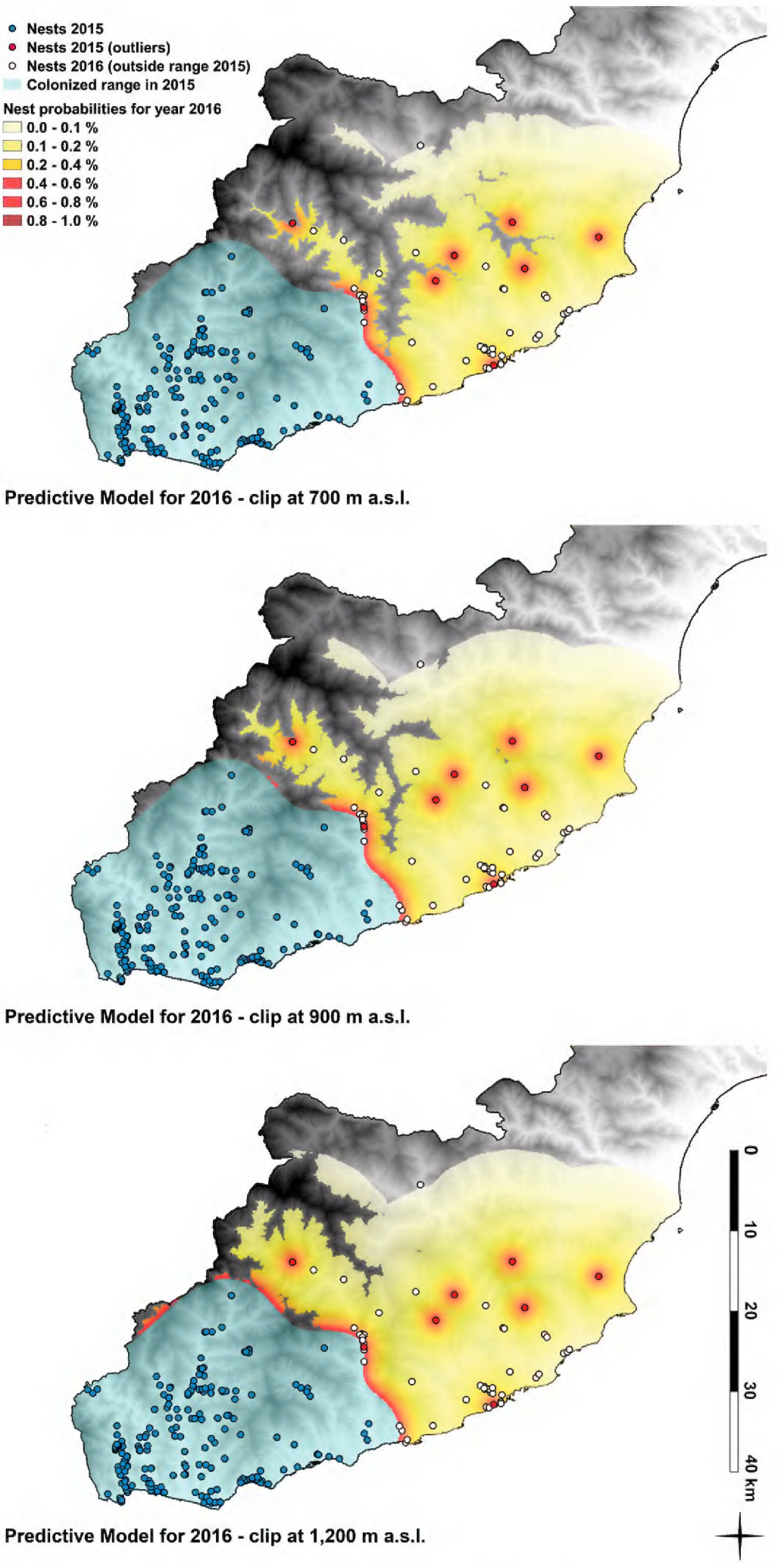
Nests 2015
Nests 2015 (outliers)
Nests 2016 (outside range 2015)
Colonized range in 2015
Nest probabilities for year 2016
0.0 - 0.1 %
0.1 - 0.2 %
0.2 - 0.4 %
0.4 - 0.6 %
0.6 - 0.8 %
0.8 - 1.0 %
Predictive Model for 2016 - clip at 700 m a.s.l.
Predictive Model for 2016 - clip at 900 m a.s.l.
Predictive Model for 2016 - clip at 1,200 m a.s.l.
0
10
20
30
40 km

Figure 3. Predictive model of expansion for year 2016 clipped at three different altitude thresholds (700 m, 900 m and 1,200 m a.s.l.). Blue dots indicate nests of year 2015 inside the continuous range, red dots nests of 2015 outside the continuous range. For 2016, only nests outside the 2015 range are reported (white). Coloured areas from red to light yellow indicate progressively less probability of colonisation in 2016.

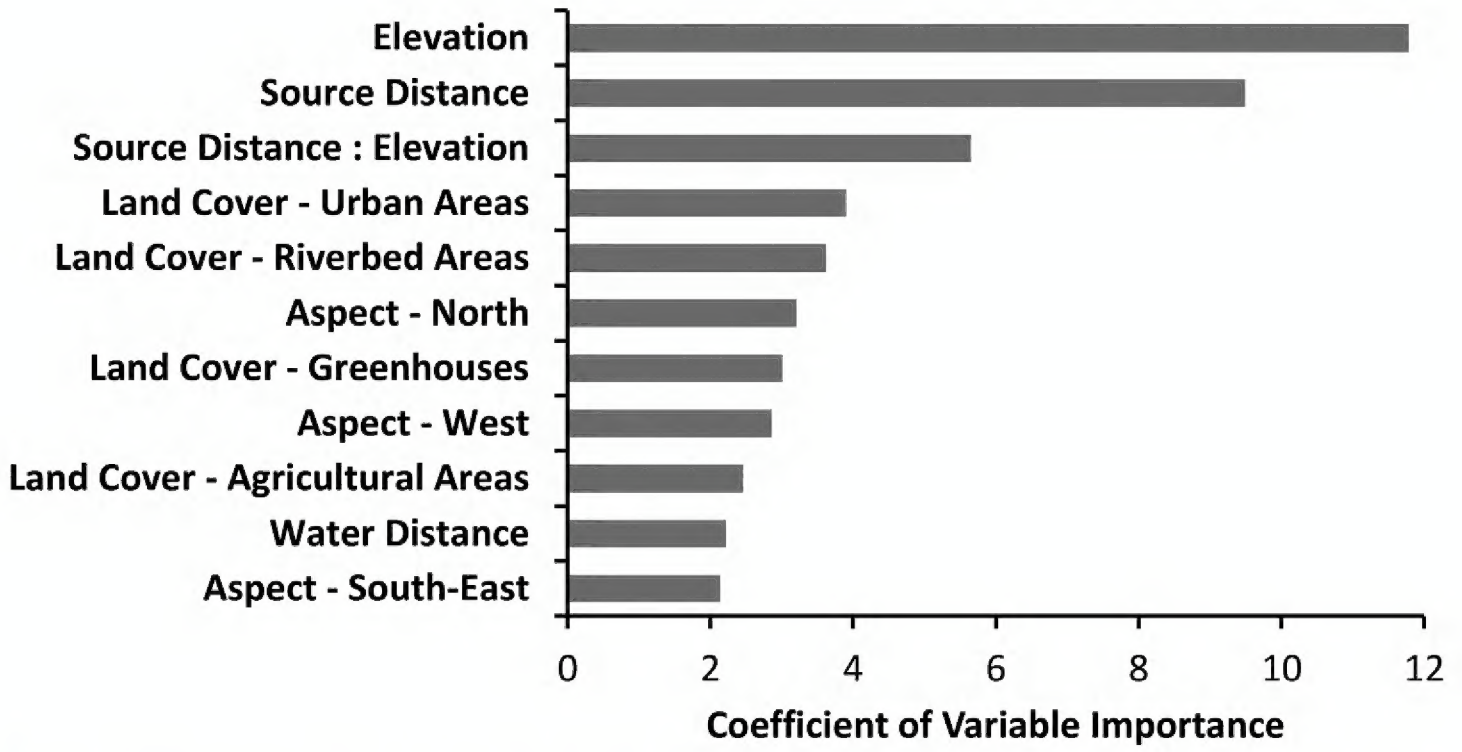

Figure 4. Coefficient scores for the explanatory variables of the GLM analysis on presence/pseudo-absence data: elevation, source distance and their interaction are the variables that contribute more in explaining spatial distribution of nests.

and probabilities associated with pseudo-presence data, therefore each model predicts quite well the spread of the yellow-legged hornet (2016: $AUC_{700\ m} = 0.78$; $AUC_{900\ m} = 0.78$; $AUC_{1200\ m} = 0.77$; 2017: $AUC_{700\ m} = 0.88$; $AUC_{900\ m} = 0.88$; $AUC_{1200\ m} = 0.88$).

The GLM analysis, which better explains the presence of hornet colonies in relation to species-dependent and environmental variables, takes into account all the considered explanatory variables and the interaction between the elevation and the distance between nests and source sites (Nagelkerke's pseudo-$R^2 = 0.60$). The variables that contribute more to the model are elevation, source distance and the interaction between these two variables (Fig. 4).

Discussion

The effective management of spreading invasive species requires the development of monitoring systems able to detect new areas colonised by the species in the short term, in order to timely extend control activities. We developed a system to evaluate the probability of yellow-legged hornet dispersal around the area where the species is present, with a progressively lower likelihood of colonisation by the species at increasing distances. The model was built with GIS software and a database with coordinates of nests located in each year. Measures of the distances of nests found in one year from a possible source of diffusion (nests of the previous year) were used to build likelihood percentages of spread at progressive distances in the subsequent year. Comparison of nest locations with pseudo-presence data confirmed that both altitude and distance from possible source sites were main factors explaining the distribution of nests. Fur-

thermore, our predictive models were tested in two years with real data (i.e. locations of nests found during control activities). In 2016 and 2017, 98–100% of yellow-legged hornet nests were found within the predicted area of expansion, supporting the validity of our modelling approach. With this method, data routinely collected during monitoring and control activities of yellow-legged hornet populations could be used as a feedback to increase the effectiveness of management strategies, allocating the available resources in relation to the probabilities of spread in the short term.

Of the nests reported in Liguria, more than a half were located within 1 km from nests of the previous year, about 90% within few kilometres (0.9–3.3 km) and nearly all within 11 km. These data indicate that new queens, despite their probable great flying ability, mostly build new colonies at short distances from their nests of origin and only few nests will be located at greater distances, due to natural diffusion on long distances or more probably to human mediated transportation. These reduced distances are in accordance with the spread of the species in Italy (18.3 ± 3.3 km/year, Bertolino et al. 2016), which is much lower than in France (78 km/year, Robinet et al. 2017). This means that local characteristics may drive species distribution and expansion; consequently, control approaches should be adaptive to local nest distributions that are a proxy of local characteristics.

The data on nests' distribution collected in these years in Italy suggest that nests are not randomly distributed in the study area, but follows aggregative patterns. This is normal in spreading populations, where areas firstly colonised by the species act as source sites for nearby areas, which are at lower densities. This is the contest where our modelling technique can be used to improve control strategies. On the contrary, areas colonised over many years by the yellow-legged hornet, such as the municipality of Andernos in France, have different local nest dynamics and, after the initial phase of invasion, nests became randomly distributed (Monceau and Thiery 2017). In this French municipality, the species reached a very high density in 2014 of 12.26 nests per km^2 with an average distance to the nearest nest of 153 m (95% confidence interval 143–163 m). This contest of high densities is completely different from the scenarios of new outbreaks or spreading populations. In the case of established populations, a control strategy that aims to limit or reduce the impact of the species should be developed. In case of new outbreaks or spreading populations, the control strategies should foresee the development of early warning and rapid response systems for early detection of nests or containment plans, as suggested by the EU (Reg. EU 1143/2014) or as performed after the invasion of Majorca in the Balearic Islands (Leza et al. 2018) or Great Britain (Defra 2017). For example, the contingency plan developed for Great Britain requires the establishment of demarcated areas (buffer areas) nearby the sites of invasion after the presence of the yellow-legged hornet has been confirmed. The early warning and rapid response approach supports the need to develop a predictive model of expansion in the short term using data collected locally: the protocol here proposed can be easily adapted and used to increase the efficiency of the monitoring activity. Intensive monitoring and control activities in a buffer area around the range of the species or new invasion outbreaks, allocated considering the different likelihood

of colonisation, might therefore allow cost-effective use of the available resources. In this regard, the situation in Liguria is ideal for developing a control strategy that foresees the identification of buffer areas to monitor with different intensity, because the species is spreading mainly through a corridor along the coastline from West to East, with the sea to the South and mountains that might act as a partial barrier to the North (Bertolino et al. 2016). These characteristics could constrain the spread of the yellow-legged hornet, thus reducing the areas that should be covered and increasing the possibility for effective monitoring. Therefore, morphologic characteristics of the environment should be considered when exporting this approach in other European areas, since monitoring and control effectiveness could be maximised by the presence of limiting factors or could be reduced by their absence.

Arthropods may jump long distances when the dispersal is human-mediated (Hastings et al. 2005, Homans and Horie 2011). An important implication of the possibility for a species to cross long distances is that it can overcome barriers, established to contain the species within the present range. For instance, nests of the yellow-legged hornet have been recorded in Europe, tens and even hundreds of kilometres away from the invasion front, thus suggesting an accidental human transportation of founders (Rome et al. 2009, Bertolino et al. 2016, Robinet et al. 2017). In 2016, only one nest was found in Veneto at about 270 km from the invaded areas in Italy, while, in 2017, some adults were observed at 140 and 170 km, respectively in the eastern part of Liguria and northern Tuscany (Lioy et al. 2018). In previous years, animals and nests were found at several tens and up to 150 km from possible sources of diffusion (Bertolino et al. 2016). Identifying natural dispersal from human-mediated transportation is not always easy. However, even considering some of long distance reports as resulting from natural dispersal would not change the validity of our simulation. In fact, we were interested in building an information system that could help plan the yearly optimal allocation of the monitoring effort, covering an area of possible expansion from the continuous range of the species. Of course, a comprehensive management strategy also requires the development of plans to find and manage sub-populations found even at considerable distances from the expansion front. This is what is usually foreseen in the surveillance protocol of an early warning and rapid response system (Britton et al. 2010, Homans and Horie 2011), a protocol that has been established in Italy by the development of a wide monitoring network with the collaboration of beekeepers (Suppl. material 5). Ideally, such surveillance system should allow the location of yellow-legged hornet nests, established from long-distance dispersal or human-mediated transportation of queens. In case of detection of new propagules, our data-informed process could help in establishing an intensive monitoring network to locate and destroy nests before a new invasion starts, as well as with the use of new technologies as the tracking of hornets with harmonic radars (Milanesio et al. 2016, 2017) or radio-telemetry (Kennedy et al. 2018).

An aspect that must be considered is the bias in nest detection, since tree leaves often hide *V. velutina* colonies. For this reason, a wide monitoring network has been developed, as well as for areas not colonised by the species and for nearby regions and

multiple sources of information have been considered (citizens, beekeepers, firefighter teams, monitoring teams, ...). Monitoring teams also continued to work in the field during autumn and winter, detecting nests that might have been previously covered by tree canopies.

The method here proposed allows the assessment of the proportion of landscape that should be surveyed over the front of the spreading range of an invasive social insect species and the intensity of the monitoring activity allocated at progressive distances. It only requires the availability of nest locations in successive years, which are a proxy of other local (either climate or environmental) characteristics, and can be improved by increasing the efficiency of data collection. This approach is different from other modelling techniques, such as climatic or habitat models widely used for invasive species (Beaumont et al. 2009, Di Febbraro et al. 2016), including the yellow-legged hornet (Ibáñez-Justicia and Loomans 2011, Villemant et al. 2011, Balmori 2015, Fournier et al. 2017, Keeling et al. 2017, Robinet et al. 2017). In fact, these models estimate the areas that could be invaded in the future, comparing climatic or habitat characteristics of such areas with niche requirements of the species, but their use in short-term management strategies is limited. This is because many of these models extrapolate the parameters from other areas with different characteristics or because they are produced at large scales, while species management is usually implemented at more local scales. These approaches are extremely important when the aim is to understand the consequences of invasion in the long term and at European level. Instead, our method estimates the likelihood of colonisation of new areas by the species in the short term, from one year to another and for the studied population, important information that could be used to improve the efficiency of local management plans for the yellow-legged hornet and other similar species that build colonial nests.

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References

Archer ME (2012) Vespine wasps of the world. Behaviour, Ecology and Taxonomy of the Vespinae. Monograph series, Volume 4. Siri Scientific Press, Manchester: 1–352.

Archer ME (1994) Taxonomy, distribution and nesting biology of the Vespa bicolor group (Hym., Vespinae). Entomologist's Monthly Magazine 130: 149–158.

Balmori A (2015) Sobre el riesgo real de una expansiòn generalizada de la Avispa Asiàtica *Vespa velutina* Lepeletier, 1836 (Hymenoptera: Vespidae) en la Penìnsula Ibérica. Boletín de la Sociedad Entomológica Aragones 56: 283–289.

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? PloS One 13: e0193085. https://doi.org/10.1371/journal.pone.0193085

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Diversity and Distributions 15: 409–420. https://doi.org/10.1111/j.1472-4642.2008.00547.x

Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F, Rome Q, Villemant C (2011) Ecological effects and management of invasive alien Vespidae. BioControl 56: 505–526. https://doi.org/10.1007/s10526-011-9389-z

Bertolino S, Viterbi R (2010) Long-term cost-effectiveness of coypu (*Myocastor coypus*) control in Piedmont (Italy). Biological Invasions 12: 2549–2558. https://doi.org/10.1007/s10530-009-9664-4

Bertolino S, Perrone A, Gola L (2005) Effectiveness of coypu control in small Italian wetland areas. Wildlife Society Bulletin 33: 714–720. https://doi.org/10.2193/0091-7648(2005)33[714:EOCCIS]2.0.CO;2

Bertolino S, Lioy S, Laurino D, Manino A, Porporato M (2016) Spread of the invasive yellow-legged hornet *Vespa velutina* (Hymenoptera: Vespidae) in Italy. Applied Entomology and Zoology 51: 589–597. https://doi.org/10.1007/s13355-016-0435-2

Braysher M (1993) Managing Vertebrate Pests: Principles and Strategies. Bureau of Resource Sciences, Australian Government Publishing Service, Canberra, 60 pp.

Britton KO, White P, Kramer A, Hudler G (2010) A new approach to stopping the spread of invasive insects and pathogens: early detection and rapid response via a global network of sentinel plantings. New Zealand Journal of Forestry Science 40: 109–114.

Calenge C (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Choi MB, Martin SJ, Lee JW (2012) Distribution, spread, and impact of the invasive hornet *Vespa velutina* in South Korea. Journal of Asia-Pacific Entomology 15: 473–477. https://doi.org/10.1016/j.aspen.2011.11.004

De Haro L, Labadie M, Chanseau P, Cabot C, Blanc-Brisset I, Penouil F (2010) Medical consequences of the Asian black hornet (*Vespa velutina*) invasion in Southwestern France. Toxicon 55: 650–652. https://doi.org/10.1016/j.toxicon.2009.08.005

Defra (2017) Pest Specific Contingency Plan for the Asian Hornet (*Vespa velutina nigrithorax*). Department for Environment Food & Rural Affairs, 37 pp.

Demichelis S, Manino A, Minuto G, Mariotti M, Porporato M (2014) Social wasp trapping in north west Italy: comparison of different bait-traps and first detection of *Vespa velutina*. Bulletin of Insectology 67: 307–317.

Di Febbraro M, Martinoli A, Russo D, Preatoni D, Bertolino S (2016) Modelling the effects of climate change on the risk of invasion by aliens squirrels. Hystrix, the Italian Journal of Mammalogy 27: 1–8.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38–49. https://doi.org/10.1017/S0376892997000088

Fournier A, Barbet-Massin M, Rome Q, Courchamp F (2017) Predicting species distribution combining multi-scale drivers. Global Ecology and Conservation 12: 215–226. https://doi.org/10.1016/j.gecco.2017.11.002

Franklin DN, Brown MA, Datta S, Cuthbertson AGS, Budge GE, Keeling MJ (2017) Invasion dynamics of Asian hornet, *Vespa velutina* (Hymenoptera: Vespidae): a case study of a commune in south-west France. Applied Entomology and Zoology 52: 221–229. https://doi.org/10.1007/s13355-016-0470-z

Gilbert M, Gregoire JC, Freise JF, Heitland W (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. Journal of Animal Ecology 73: 459–468. https://doi.org/10.1111/j.0021-8790.2004.00820.x

Grosso-Silva JM, Maia M (2012) *Vespa velutina* Lepeletier, 1836 (Hymenoptera, Vespidae), new species for Portugal. Arquivos Entomolóxicos 6: 53–54.

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. Ecology Letters 8: 91–101. https://doi.org/10.1111/j.1461-0248.2004.00687.x

Hauser CE, McCarthy MA (2009) Streamlining 'search and destroy': cost-effective surveillance for invasive species management. Ecology Letters 12: 683–692. https://doi.org/10.1111/j.1461-0248.2009.01323.x

Haxaire J, Bouguet JP, Tamisier JP (2006) *Vespa velutina* Lepeletier, 1836, une redoutable nouveauté pour la faune de France (Hym., Vespidae). Bulletin de la Société entomologique de France 111: 194.

Homans F, Horie T (2011) Optimal detection strategies for an established invasive pest. Ecological Economics 70: 1129–1138. https://doi.org/10.1016/j.ecolecon.2011.01.004

Ibáñez-Justicia A, Loomans AJ (2011) Mapping the potential occurrence of an invasive species by using CLIMEX: case of the Asian hornet (*Vespa velutina nigrithorax*) in the Netherlands. In: Jan Bruin (Ed.) Proceedings of the Netherlands Entomological Society Meeting 22. Ede (Netherlands), December 2010. Nederlandse Entomologische Vereniging, Amsterdam, 39–46.

Keeling MJ, Franklin DN, Datta S, Brown MA, Budge GE (2017) Predicting the spread of the Asian hornet (*Vespa velutina*) following its incursion into Great Britain. Scientific Reports 7: 6240. https://doi.org/10.1038/s41598-017-06212-0

Kennedy PJ, Ford SM, Poidatz J, Thiéry D, Osborne JL (2018) Searching for nests of the invasive Asian hornet (*Vespa velutina*) using radio-telemetry. Communications Biology 1: 88. https://doi.org/10.1038/s42003-018-0092-9

Leza M, Miranda MA, Colomar V (2018) First detection of *Vespa velutina nigrithorax* (Hymenoptera: Vespidae) in the Balearic Islands (Western Mediterranean): a challenging study case. Biological Invasions 20: 1643–1649. https://doi.org/10.1007/s10530-017-1658-z

Lioy S, Laurino D, Manino A, Porporato M (2018) *Vespa velutina* in Italy: an update on the management activities and on the impact of the species on honey bee colonies and bio-

diversity. In: Proceeding of the Velutina Task Force meeting, Bilbao (Spain), June 2018: 19–20. https://coloss.org/publications/proceedings-minutes

Liu ZR, Chen SG, Zhou Y, Xie CH, Zhu BF, Zhu HM, Liu SP, Wang W, Chen HZ, Ji YH (2015) Deciphering the Venomic Transcriptome of Killer-Wasp *Vespa velutina*. Scientific Reports 5: 9454. https://doi.org/10.1038/srep09454

Marris G, Brown M, Cuthbertson A (2011) GB non-native organism risk assessment for *Vespa velutina nigrithorax*. http://www.nonnativespecies.org

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C, Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299–314. https://doi.org/10.1007/s10530-015-1013-1

Milanesio D, Saccani M, Maggiora R, Laurino D, Porporato M (2016) Design of an harmonic radar for the tracking of the Asian yellow-legged hornet. Ecology and Evolution 6: 2170–2178. https://doi.org/10.1002/ece3.2011

Milanesio D, Saccani M, Maggiora R, Laurino D, Porporato M (2017) Recent upgrades of the harmonic radar for the tracking of the Asian yellow-legged hornet. Ecology and Evolution 7: 4599–4606. https://doi.org/10.1002/ece3.3053

Monceau K, Maher N, Bonnard O, Thiery D (2013) Predation pressure dynamics study of the recently introduced honeybee killer *Vespa velutina*: learning from the enemy. Apidologie 44: 209–221. https://doi.org/10.1007/s13592-012-0172-7

Monceau K, Thiery D (2017) *Vespa velutina* nest distribution at a local scale: An 8-year survey of the invasive honeybee predator. Insect Science 24: 663–674. https://doi.org/10.1111/1744-7917.12331

Monceau K, Bonnard O, Thiery D (2014) *Vespa velutina*: a new invasive predator of honeybees in Europe. Journal of Pest Science 87: 1–16. https://doi.org/10.1007/s10340-013-0537-3

Porporato M, Manino A, Laurino D, Demichelis S (2014) *Vespa velutina* Lepeletier (Hymenoptera Vespidae): a first assessment two years after its arrival in Italy. Redia 97: 189–194.

QGIS Development Team (2015) QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://qgis.org/it/site/

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org/

Regione Liguria (2015) Uso del Suolo sc. 1:10000 – ed. 2015. Regione Liguria, Settore Informatica, Segreteria Generale. http://www.cartografia.regione.liguria.it

Robinet C, Suppo C, Darrouzet E (2017) Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. Journal of Applied Ecology 54: 205–215. https://doi.org/10.1111/1365-2664.12724

Rodríguez-Flores MS, Seijo-Rodríguez A, Escuredo O, Seijo-Coello MDC (2018) Spreading of *Vespa velutina* in northwestern Spain: influence of elevation and meteorological factors and effect of bait trapping on target and non-target living organisms. Journal of Pest Science. Advance online publication. https://doi.org/10.1007/s10340-018-1042-5

Rome Q, Muller F, Gargominy O, Villemant C (2009) Bilan 2008 de l'invasion de *Vespa velutina* Lepeletier en France (Hymenoptera: Vespidae). Bulletin de la Société Entomologique de France 114: 297–302.

Rome Q, Muller FJ, Touret-Alby A, Darrouzet E, Perrard A, Villemant C (2015) Caste differentiation and seasonal changes in *Vespa velutina* (Hym.: Vespidae) colonies in its introduced range. Journal of Applied Entomology 139: 771–782. https://doi.org/10.1111/jen.12210

Rome Q, Dambrine L, Onate C, Muller F, Villemant C, García-Pérez A, Maia M, Carvalho Esteves P, Bruneau E (2013) Spread of the invasive hornet *Vespa velutina* Lepeletier, 1836, in Europe in 2012 (Hym.,Vespidae). Bulletin de la Société entomologique de France 118: 21–22.

Sauvard D, Imbault V, Darrouzet E (2018) Flight capacities of yellow-legged hornet (*Vespa velutina nigrithorax*, Hymenoptera: Vespidae) workers from an invasive population in Europe. PLoS ONE 13: e0198597. https://doi.org/10.1371/journal.pone.0198597

Sharov AA, Liebhold AM (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. Ecological Applications 8: 1170–1179. https://doi.org/10.1890/1051-0761(1998)008[1170:MOSTSO]2.0.CO;2

Shatz AJ, Rogan J, Sangermano F, Miller J, Elmes A (2016) Modeling the risk of spread and establishment for Asian longhorned beetle (*Anoplophora glabripennis*) in Massachusetts from 2008–2009. Geocarto International 31: 813–831. https://doi.org/10.1080/10106049.2015.1086901

Sing T, Sander O, Beerenwinkel N, Lengauer T (2005) ROCR: visualizing classifier performance in R. Bioinformatics 21: 3940–3941. https://doi.org/10.1093/bioinformatics/bti623

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America 98: 1095–1100. https://doi.org/10.1073/pnas.98.3.1095

Sumner S, Law G, Cini A (2018) Why we love bees and hate wasps. Ecological Entomology 43: 836–845. https://doi.org/10.1111/een.12676

Tabar AI, Chugo S, Joral A, Lizaso MT, Lizarza S, Alvarez-Puebla MJ, Arroabarren E, Vela C, Lombardero M (2015) *Vespa velutina nigritorax*: a new causative agent for anaphylaxis. Clinical and Translational Allergy 5: P43. https://doi.org/10.1186/2045-7022-5-S3-P43

Ueno T (2014) Establishment of the invasive hornet *Vespa velutina* (Hymenoptera: Vespidae) in Japan. International Journal of Chemical, Environmental and Biological Sciences 2: 220–222.

Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F, Rome Q (2011) Predicting the invasion risk by the alien bee-hawking Yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. Biological Conservation 144: 2142–2150. https://doi.org/10.1016/j.biocon.2011.04.009

Supplementary material 1

Predictive model of expansion (2017)

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

Data type: statistical data

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Supplementary material 2

Predictive model of expansion (2018)

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

Data type: statistical data

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Supplementary material 3

Areas to be monitored for the predictive models of year 2017

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

Data type: statistical data

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Supplementary material 4

Areas to be monitored for the predictive models of year 2018

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

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Supplementary material 5

Monitoring network developed by LIFE STOPVESPA project in Liguria and Piedmont regions (Italy)

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

Data type: statistical data

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Supplementary material 6

Database of *Vespa velutina* nests discovered in Liguria region (Italy) in the period 2013–2017

Authors: Simone Lioy, Aulo Manino, Marco Porporato, Daniela Laurino, Andrea Romano, Michela Capello, Sandro Bertolino

Data type: statistical data

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